The effect of fishing on demersal fish community dynamics: an hypothesis

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Fishing acts like a predator; it alters the extent of competition and allows the coexistence of competitive species. To test this hypothesis, several component elements are addressed. The variability of biomass in demersal fish communities is analysed to seek evidence that biotic interactions play a role in community dynamics. Spatial segregation as a result of a fishery's removal in several communities is analysed to test whether there are differences in coexistence or segregation. Previous studies of the demersal fish community of the Scotian Shelf revealed that the coefficient of variation for total biomass over time was lower than that for individual species. Similarly, as shown in this paper, variability of biomass in the demersal fish assemblages of the Bay of Biscay and the Gulf of Lions (France) are characterized by the same patterns. This pattern is interpreted as the effects of interactions between species (predation, competition) that involve energy limitation within the systems. Also, spatial segregation among species is related to fishing intensity. First, differences in spatial segregation between the Bay of Biscay and the Gulf of Lions, as measured by the slopes of the species area curves, are significant. Spatial segregation decreases from the least harvested systems to the most harvested ones when data from several systems are compared. These analyses indicate that biotic interactions play a significant role in the dynamics of demersal fish communities and that decreases in the spatial segregation of species can be associated with increased fishing. These results are consistent with the hypothesis that fishing and predation have similar effects on fish communities.

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Introduction

Recently there have been great improvements in our understanding of community level changes in response to fishing (Hall, 1999). However, theory to explain observed community patterns remains limited (May *et al.*, 1979; Pimm and Hyman, 1987; Wilson *et al.*, 1991). The main theories developed to explain community dynamics involve abiotic environmental processes (Conover *et al.*, 1995; Ottersen and Sundby, 1995), biotic processes, or a balance between both types of process (see Barbault, 1992, and Huston, 1994, for a general review).

According to Levine (1976) and Vandermeer (1980), in communities regulated by interspecific interactions, a high intensity of predation can alter the strength of competitive interactions and allow for increased

coexistence of competitive species. Assuming that exploitation by fishing would have similar effects, fish communities subject to various levels of fishing intensity can be examined to search for such impacts. To probe this hypothesis, two preliminary questions should be addressed: (1) Is there evidence that biotic interactions play a role in the dynamics of demersal fish communities? (2) Are there differences in the coexistence or segregation of fish species that are related to the intensity of removal by a fishery?

Hennemuth (1979); Murawski *et al.* (1991) and Duplisea *et al.* (1997) showed that the temporal variability of the total biomass of demersal fish is lower than that of individual fish species on the Georges Bank, in the Gulf of Maine and over the Scotian Shelf. Using energy limitation as one explanatory factor (Steele, 1965), Hennemuth interpreted this observation

Table 1. Number of scientific surveys, total number of trawls, and the number of total landing years from fisheries in identified areas.

	Bay of Biscay	Gulf of Lions	Shelf off French Guyana
Surveys	7	9	1
Trawl hauls	866	618	98
Landing years	3	9	1

as validation of the effects of competition and predation in relationships among the various species of these communities. In the same way, Duplisea *et al.* (1997) concluded that this pattern was evidence of energy limitation at the combined species level. To address the first question, data sets from scientific surveys carried out in the Bay of Biscay and in the Gulf of Lions (France) were used in this study to compare the temporal variability of the total biomass demersal fish with that of individual species.

Several studies have demonstrated that competition contributes to the spatial segregation of fish species (Finger, 1982; Weisberg, 1986; Wang and Tzeng, 1997; Vehanen *et al.*, 1999). If fishing promotes increases in local coexistence, then spatial segregation caused by competition would be expected to decrease with increasing fishing pressure. To address the second question, the slopes of species-area curves for the Bay of Biscay and the Gulf of Lions are calculated to provide an index of spatial segregation (Whittaker, 1960). In practice, spatial segregation is defined as the degree of species change from one trawl to another. Harvesting level is measured by productivity, i.e. catches by the fisheries (Caddy *et al.*, 1995). This analysis is extended here to studies of more ecosystems, one from Kenya (McClanahan, 1994) and one from the shelf off French Guyana. With the expanded collection of systems it is possible to determine whether spatial segregation among species declines with exploitation rate.

Material and methods

Data

Several independent sets of data were used for this study (Table 1). The demersal fish assemblages represented are broadly distributed geographically (Figure 1). Seven scientific surveys were carried out in the Bay of Biscay (43–49°N, off France) for the direct evaluation of demersal stock abundance in October/November of every year from 1987–1990 and in 1992, 1994, and 1995. Data for 101–142 hauls are available for each survey. The second set of data is from nine scientific surveys carried out in the Gulf of Lions for the direct evaluation
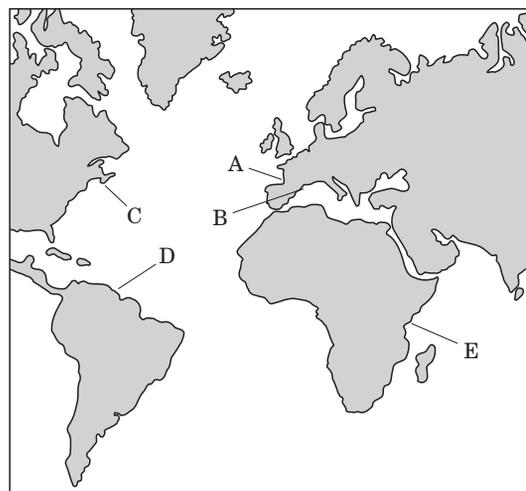
Figure 1. Areas for which data were used in this study – A: Bay of Biscay; B: Gulf of Lions; C: Scotian Shelf; D: shelf off French Guyana; E: Kenyan lagoons.

of demersal fish stock abundance in May/June of 1983, 1985–1987, 1992, and 1994–1997. Between 57 and 110 hauls are available for this data set annually. The third set of data comes from a scientific survey carried out in October 1994 on the shelf off French Guyana.

Hauls were made randomly by depth and the number of hauls is the same in each stratum. Survey procedures for the Bay of Biscay are provided in ICES (1991) and Amara *et al.* (1998). Surveys for the Gulf of Lions are described by Gaertner *et al.* (1998) and Bertrand *et al.* (1997). The survey carried out off French Guyana is described by Nerini (1994).

The annual landings of demersal fish from the Gulf of Lions and the Bay of Biscay are available from 1983–1989 (FAO, 1991) and from 1982 and 1984 (Dardignac, 1988). The landings of the French Guyana fisheries in 1993 are estimated from the works of Lemoine *et al.* (1982) and Blanchard (in press).

Biomass variability

As a partial test of whether biotic interactions play a role in community dynamics, the variabilities of total biomass and of biomass by species were compared. As biomass is not equally distributed in all strata, the total biomass was estimated for each scientific survey as the sum of the species biomass divided by the trawled area for three groups of homogeneous strata. Then the mean biomass was calculated for the three groups. The trawled area is the product of the ship's speed, the trawling time, the horizontal width of the trawl opening, and the number of hauls.

The coefficient of variation of biomass in time was used to assess variability. It is computed for each

individual species (CVi) and for the sum of species (CVt):

$$CV = (100\sigma)/\bar{x}$$

where σ is the standard deviation and $\bar{x}$ is the mean biomass. Only those species present in the samples for all years were used in the calculations because a zero value in some years artificially increases the CV.

Spatial segregation

Spatial segregation is compared among several systems to test whether differences of coexistence can be related to the level of exploitation by fisheries. Species-area curves are fitted to estimate the degree of segregation, according to the equation used by Rosenzweig (1995):

$$S = aA^{\beta}$$

where S is the species richness, A the trawled area, β the slope and index of spatial segregation and a is a constant related to overall species richness. Species-area curves are determined by the accumulation of species for every annual survey: species are counted in one trawl and the new species encountered in each of the following trawls are added, step by step. The annual curves are then aggregated within each area (e.g. the Bay of Biscay and the Gulf of Lions). A log-transformation (base 10) linearizes the species-area curve. Therefore β, the slope of the linear regression, is calculated as an index of segregation. The covariance analysis allows comparison of the slopes (and segregation) between two areas.

McClanahan (1994) provided species-area curves for a Kenyan fish community in an area protected from fishing, an unprotected one, and in an intermediate area; the resulting values are given here for comparison.

For the shelf off French Guyana, a species-area curve is fitted for the only year for which data are available (1994). The β value for the Kenyan protected area provides an index of segregation for an unfished community. The slopes of species-area curves for the Bay of Biscay, the Gulf of Lions, the shelf off French Guyana and the unprotected Kenyan lagoon provide indices of segregation for the respective levels of associated fishing intensity. These are plotted to investigate the relationship between spatial segregation and removal by a fishery.

Fisheries productivity

In order to examine differences in spatial segregation between communities as a function of fishing intensity we needed a measure of the latter. Here we used the productivity of a fishery as the level of harvesting intensity.

A global index of the intensity of harvesting was computed on the basis of the work of Charbonnier and Garcia (1985) and Caddy et al. (1995), wherein it is shown that the landings per unit of surface area increase with fishing effort in the Mediterranean Sea. This being the case, the productivity of a fishery, expressed as the annual landings of demersal fish per unit area of the surface of the continental shelf, may be used as an index of harvest intensity. This measure expresses the intensity as the biomass harvested by unit area.

Results

Biomass variability

The temporal variability of the total biomass of demersal fish was compared with that of the biomass of individual species in the Bay of Biscay and in the Gulf of Lions (Table 2). In the Bay of Biscay, 65 species of demersal fish were present during all scientific surveys. The mean of the total biomass for these species is 0.97 g m^{-2}, with a CVt of 32.3%, and the CVi varies between 18.4–140.5%. Of the 65 species, 62 had a coefficient of variation higher than the coefficient of variation of the total biomass. In the Gulf of Lions, 45 species were present during all scientific surveys. The mean of the total biomass was 0.84 g m^{-2}, with a CVt of 40.3%, and a CVi that varied from 24.1–186.7%. Of the 45 species, 38 had a coefficient of variation higher than the coefficient of variation of the total biomass.

The temporal variability of the total biomass is lower than that for individual species in both geographic areas, as shown in previous studies. This result indicates that biotic interactions between species likely play a role in the dynamics of these communities of demersal fish.

Spatial segregation

The values of the slope for the species-area curves showed patterns that were expected when several demersal fish assemblages were compared. A relationship between segregation and fishery productivity was apparent when presented graphically.

Species-area curves provided significant fits for the data from the Bay of Biscay and the Gulf of Lions (Figure 2, respectively $r^2 = 0.77$ and $r^2 = 0.87$, $p < 0.01$). The slope value, β, of the linearized models was 0.29 for the Gulf of Lions and 0.35 for the Bay of Biscay. The slopes differ significantly ($p < 0.01$). The curve was steeper in the Bay of Biscay than in the Gulf of Lions, showing that there were higher levels of segregation. As the regression seems to overestimate species richness (S) for small surface areas (A), the linear model was tested with A log-transformed and S not. In that case, the goodness-of-fit was lower (coefficients of determination

Table 2. List of species and the coefficients of variation for individual species and total biomass in the demersal fish assemblages. Emboldened species CVi are smaller than the CVt of total biomass.

Species	Bay of Biscay CV	Gulf of Lions CV	Species	Bay of Biscay CV	Gulf of Lions CV
Ammodytes tobianus	118.9		*Merluccius merluccius*	42.6	47.4
Argentina sphyraena	68.6	101.2	*Merlangius merlangus*	39.6	
Argentina silus	82.0		*Microstomus kitt*	49.0	
Arnoglossus laterna	79.2	80.0	*Microchirus variegatus*	72.4	65.3
Arnoglossus rueppelli		82.1	*Molva molva*	42.6	
Arnoglossus thori		50.9	*Mullus barbatus*		71.6
Arnoglossus imperialis	39.0		*Mullus surmuletus*	80.9	60.9
Aspitrigla cuculus	48.3	**35.5**	*Pagellus acarne*	85.5	66.4
Aspitrigla obscura		76.4	*Pagellus bogaraveo*		84.5
Bathysolea profundicola	117.1		*Pagellus erythrinus*		50.3
Blennius ocellaris		**35.9**	*Phycis blennoides*	66.1	68.8
Boops boops	101.9	71.4	*Phrynorhombus norvegicus*	114.5	
Buglossidium luteum	111.0	121.9	*Pleuronectes platessa*	66.0	
Callionymus lyra	123.1		*Pollachius pollachius*	121.9	
Callionymus maculatus	92.6		*Pomatoschistus minutus*	122.2	
Capros aper	69.6	162.2	*Psetta maxima*	88.8	
Cepola rubescens	59.4	79.2	*Raja clavata*	45.4	50.2
Chimaera monstrosa	76.9		*Raja fullonica*	124.5	
Citharus macrolepidotus		50.0	*Raja montagui*	50.4	
Coelorhynchus coelorhynchus	81.9		*Raja naevus*	56.0	
Conger conger	44.9	**27.4**	*Scorpaena elongata*		75.8
Dicentrarchus labrax	73.5		*Scorpaena notata*		60.8
Dicologoglossa cuneata	55.9		*Scyliorhinus canicula*	**31.3**	76.4
Diplodus annularis		94.8	*Serranus cabrila*		45.2
Echiichthys vipera	43.8		*Serranus hepatus*		61.7
Enchelyopus cimbrius	93.7		*Solea vulgaris*	43.4	52.5
Etmopterus spinax	97.4		*Sparus aurata*	127.5	
Eutrigla gurnardus	103.5	53.1	*Spondyliosoma cantharus*	61.8	
Gadiculus argenteus	108.6		*Squalus acanthias*	133.5	126.4
Galeus melastomus	91.3	84.4	*Syngnathus acus*	140.2	
Helicolenus dactylopterus	49.8	105.1	*Torpedo marmorata*	85.6	
Hyperoplus lanceolatus	130.9		*Trachinus draco*	56.6	57.6
Labrus bergylta	71.4		*Trigla lucerna*	69.3	74.0
Lepidorhombus boscii	50.8	**24.1**	*Trigla lyra*		78.1
Lepidorhombus whiffiagonis	36.6		*Trigloporus lastoviza*	78.4	72.0
Lepidotrigla cavillone		48.8	*Trisopterus minutus capelanus*		28.8
Lesueuriogobius friesii	97.7		*Trisopterus luscus*	71.6	
Lophius budegassa	**32.1**	**31.2**	*Trisopterus minutus*	**18.4**	
Lophius piscatorius	49.6	65.4	*Uranoscopus scaber*		**37.6**
Macrorhamphosus scolopax	140.5	186.7	*Zeus faber*	91.4	40.3
Malacocephalus laevis	63.4				
Melanogrammus aeglefinus	102.8		**CVt**	**32.3**	**40.3**

r^2 are 0.74 and 0.82), and the slope of the curves remained steeper for the Bay of Biscay than for the Gulf of Lions.

The slopes of the species-area curves are shown to compare harvested fish communities, protected fish communities, and intermediate communities in Kenya (Figure 3). The slopes of the species-area curves increase from the unprotected area to the intermediate area and then to the protected area, respectively from 0.27 to 0.31 to 0.38. Spatial segregation (as measured by the slope) increased when fishing effort decreased. Local coexistence was highest in the most exploited area and lowest in the protected area.

Finally, Figure 4 shows the relationship between the slope of the species-area curve for each system and the corresponding fishery productivity. The slope decreases when the fishery productivity increases, a fact also established by the data in Table 3. The slope is steepest for the Kenyan protected area (0.38), decreases for the Bay of Biscay (0.35) and for the shelf off French Guyana (0.33), and finally is lowest in the Gulf of Lions (0.29), the area with the highest level of fishing.

Therefore, there were clear differences between spatial segregation in the areas studied (and therefore between coexistence in each). The differences are related to the extent of removal by the fishery in each area. Spatial
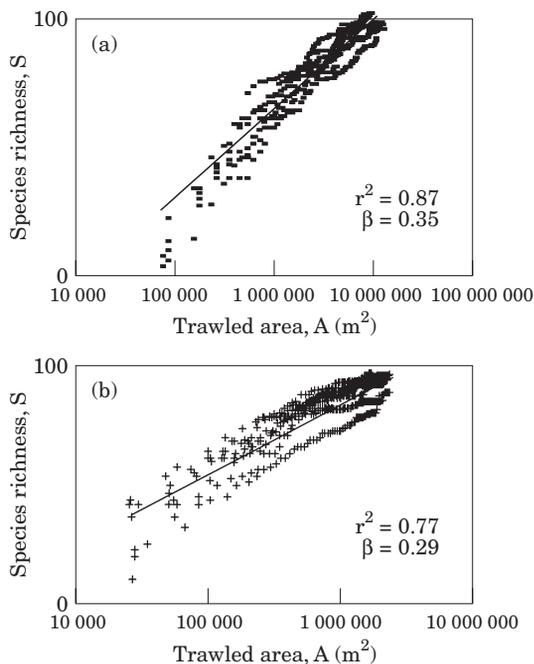
Figure 2. Number of species shown as a function of area sampled (m^2) during all the surveys in (a) the Bay of Biscay and (b) the Gulf of Lions. β is the slope of the regression and an index of spatial segregation.
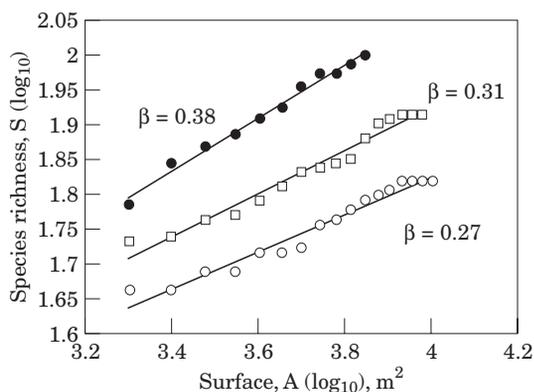
Figure 3. Number of species (log$_{10}$) shown as a function of area (log 10, m) sampled in protected (dots), transition (squares) and unprotected reef (circles) in Kenya (after McClanahan, 1994).

segregation decreases progressively from unexploited systems to those that are harvested more extensively.

Discussion

The results of the study revealed higher biomass variation for individual demersal fish species than for their total biomass in both the Bay of Biscay and the Gulf of Lions. Duplisea *et al.* (1997) observed the same pattern over the Scotian Shelf using scientific survey data. They
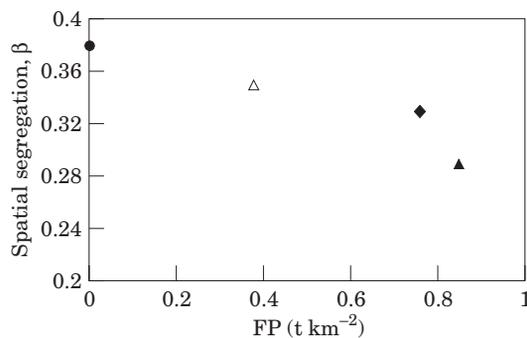
Figure 4. Relationship between spatial segregation (β) and fishery productivity FP (total landings by unit of area in t km^{-2}) in the Gulf of Lions (black triangle), the shelf off French Guyana (diamond), the Bay of Biscay (open triangle) and in a Kenyan coral reef lagoon (circle).

interpreted the low variability in total biomass relative to the high variability for individual species using Steele's (1965) hypothesis of energy limitation, according to which the carrying capacity of the ecosystem forces trophic interactions between species. Because the total biomass variability is lower than the biomass variability of individual species in both regions studied, interactions between species are expected to play a role in the dynamics of these communities. In addition to biotic interactions, Tilman (2000) suggests that a mathematical artefact may also be involved in reducing the variability in the total biomass. If biotic interactions are equal (in number and strength), a community with more species than another will be characterized by a lower total variability as a result of random compensations. However, the coefficient of variation of the total biomass is lower for the Bay of Biscay community than for that in the Gulf of Lions if computed with the same number of species (the 45 most abundant species) in both systems (CVt is 31.9 for the Bay of Biscay and 37 for the Gulf of Lions). The higher value for the Gulf of Lions can be explained by there being fewer biotic interactions, corresponding to the higher fishing pressure. This strengthens the role of the biotic interactions in causing the low variability in total biomass as well as the decrease in interactions by exploitation.

In the work reported here, the specific nature and the strength of biotic interactions are not analysed. To address the nature of such biotic processes, studies would have to focus on fewer species. For example, studies of population dynamics have demonstrated the role of competition among reef species (for a review, see Jennings and Kaiser, 1998). A study of strength of interaction not only requires concerted focus on few species, but also requires more data on trophic relationships (McCann *et al.*, 1998; Berlow, 1999; Berlow *et al.*, 1999).

Table 3. Mean annual demersal fisheries landings (L, t), area of the continental shelf (A, km^2), fishery productivity (FP=L/A, t km^{-2}), and spatial segregation of species (β).

Parameter	Bay of Biscay	Gulf of Lions	Shelf of French Guyana	Protected Kenyan lagoon
L (t)	64 499*	11 860‡	30 518	0
A (km^2)	170 000	14 000	40 000	—
FP (t km^{-2})	0.38	0.85	0.76	0
β	0.35	0.29	0.33	0.38†

*Dardignac (1988)
†McClanahan (1994)
‡FAO (1991)

Several empirical and experimental works have demonstrated that competition can cause spatial segregation of fish species (Finger, 1982; Weisberg, 1986; Wang and Tzeng, 1997; Vehanen *et al.*, 1999). Reduced competition would result in localized coexistence among competing species (Levine, 1976; Vandermeer, 1980; Huston, 1994). If so, spatial segregation should decline. Therefore, it is of no surprise that the slope of the species-area curve is low where the fishing pressure is the highest (in the Gulf of Lions) and highest in the protected area of Kenya. Moreover, in Kenya, the slope increases in the progression from unprotected to intermediate to protected areas. Clearly, there are differences in spatial segregation (and coexistence) in different communities that are related to levels of fishery exploitation.

McClanahan (1994), in his work on Kenyan lagoons, focused on the number of species and not on the slope of the species-area curves. Despite the fact that all had the same complexity of reef (Figure 3), he found species richness in the unprotected area to be lower than in the other two areas. Moreover, in the unprotected area, the density of individual species was lower than in the other areas. He concluded that localized extirpation of species is related to fishing. Species richness is the intercept of the linearized species-area curves (related to constant a) whereas spatial segregation is related to the slope. In a linear regression model, the slope and the intercept are negatively correlated. Thus, a decrease in species richness would be expected where spatial segregation increases. In such a case, it would be difficult to interpret variations in both parameters of the species-area model. Despite this negative mathematical correlation, both parameters decrease when harvesting increases, as shown by McClanahan (1994). Variations in the two parameters can therefore be interpreted as an effect of fishing. Moreover, local or population extinction and reduced densities are consistent with a decrease in the intensity of competition and, consequently, with increased coexistence.

In the current work, species richness was not compared among systems (Bay of Biscay, Gulf of Lions, shelf off French Guyana) because the dynamics of diversity at this scale is probably determined by historical and biogeographic factors as well as ecological ones (Huston, 1994; Rosenzweig, 1995). Further studies are needed to test whether the effect of fishing on species richness can be observed at a biogeographic scale.

The causal relationship between fishery productivity and fishing effort is assumed by Charbonnier and Garcia (1985) on the basis of an observed relationship in the Mediterranean Sea: there, fishery productivity increases with fishing effort (expressed per unit area). This relationship will have to be observed in the other systems to allow the use of fishery productivity as a proxy for the fishing pressure. However, even before such composite analyses are made, those reported here give clear indications that harvesting alters competitive interactions and spatial segregation.

The level of harvesting sustained by a community is described in this study as the total annual landings of demersal fish per unit area of continental shelf surface. Caddy *et al.* (1995, 1998) observed an increase in such an index in the Mediterranean Sea. They considered this increase to be influenced by either nutrient enrichment brought by anthropogenic runoff or an increase in fishing effort. Whatever its cause, such an increase is observed only in the landings of the Gulf of Lions for the three last years of the time-series (1987, 1988, and 1989). When these years are removed from the calculation, fishery productivity decreases from 0.85 to 0.61 t km^{-2}, but the relationship between spatial segregation and fishing intensity remains.

According to Caswell and Cohen (1993) and Rosenzweig (1995), the slope of the "mainland species-area curve" is a measure of beta diversity. Most agree that diversity dynamics may differ across scales (Ricklefs, 1987; Caswell and Cohen, 1993; Huston, 1994; Rosenzweig, 1995). Patterns of species-area curve at a mainland scale are determined by ecological processes, and beta diversity (between-habitat diversity) should depend on habitat heterogeneity (Rosenzweig, 1995). The Gulf of Lions and the Bay of Biscay are of such a scale and involve various habitats. According to Shmida and Wilson (1985), a low beta diversity value may result in a

homogeneous area (of single habitat) whereas a high value may be associated with a zoned (heterogenous) area of diverse habitats. This result could lead us to conclude that the Bay of Biscay is a more heterogeneous system than the Gulf of Lions. Spatial segregation is defined here as the degree of species change along a given physiographic gradient (Whittaker, 1960). Many demersal fish assemblages are determined primarily by depth (Iglesias, 1981; Overholtz and Tyler, 1985; Roel, 1987; Mahon and Smith, 1989; Daan *et al.*, 1990; Gomes *et al.*, 1995; Poulard and Boucher, 1997; Gaertner *et al.*, 1998). A depth gradient should therefore account for most of the physical heterogeneity of an area relevant to the characterization of fish communities. The depth of area sampled extends from 20–600 m in both the Bay of Biscay and the Gulf of Lions. Because the depth gradients are similar in both regions, physical heterogeneity can also be assumed to be similar. This being the case, the beta diversity difference observed in this study is more likely attributable to lessened interaction as a direct consequence of fishing than it is to differences in physical heterogeneity.

Conclusion

Two points from this study need emphasis. Lower variability in total biomass than for individual species has been shown for the Scotian Shelf and now for the Bay of Biscay and the Gulf of Lions. This pattern indicates that interspecific interactions play a role in the dynamics of species, leading to compensation and more stability at a community level than among individual species. This pattern may be expected in many demersal fish assemblages. Furthermore, spatial segregation decreases when levels of harvesting increase. These two results are consistent with the hypothesis that harvesting leads to an altering of competitive relationships and to a level of coexistence not expected under pristine (unfished) conditions. More work is needed to better validate this conclusion, but initial results clearly show that the hypothesis cannot be rejected. The slope of species-area curves offers a broad indicator of the impact of fishing with theoretical underpinnings of the processes involved.

Acknowledgements

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